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Do non-myrmocophilic epiphytes influence community structure of arboreal ants?

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Abstract

In a one-year-survey in Panama we examined the influence of a tree crown's epiphyte assemblage on its ant fauna. Ants were collected with various types of insect traps in 25 crowns of *Annona glabra* trees. The study trees were assigned to three different categories according to their epiphyte load, and to an epiphyte-free control group. We collected 22,335 specimens of 91 morphospecies, 32 genera and six subfamilies. By far the most abundant species was *Solenopsis zeteki*, a minute Myrmicinae, which was found in each of the 25 study trees. Many other species were also rather common and widely distributed throughout the study area. Only six species were singletons. Measures of α- and β-diversity, species abundance and species composition were not affected by the epiphyte load of a tree. We also made direct *in situ* observations of ants on 34 additional *Annona glabra* trees with and without epiphytes. Workers were attracted with tuna and sugar baits, and interspecific interactions and nesting sites were recorded. In total, 40 species of ants were found, all of which had also been collected in the traps. Almost half of the colonies (48%) used dead wood as nesting substrate, while 29% nested in epiphytes. Consistent with the results of the trap survey, the epiphyte load of the study trees had no influence on ant species richness and composition, but a significant correlation between ant abundance and epiphyte load was detectable. In both data sets, the lack of associations between ant species indicated that the ant assemblages were not structured in a mosaic-like fashion. We conclude that epiphytes do hardly influence the composition of ant assemblages in the studied tree crowns, probably because arboreal ants are highly opportunistic with respect to their host plants.

In einer einjährigen Studie wurde der Einfluss von Epiphytengemeinschaften in Baumkronen auf die dort lebende Ameisenfauna untersucht. Die Ameisenfauna wurde mit zwei unterschiedlichen Methoden erfasst. Zum einen wurden mit verschiedenen Arthropodenfallen *Annona glabra* Bäume beprobt, die gemäß ihres Epiphytenbewuchses in drei verschiedene Kategorien und eine unbewachsene Kontrollgruppe eingeteilt wurden. Insgesamt wurden 22.335 Individuen aus 91 Arten gefangen, die 32 Gattungen und sechs Unterfamilien zuzuordnen waren. Die häufigste Art, *Solenopsis zeteki*, eine winzige Myrmicinae, wurde auf allen 25 beprobten Bäumen gefunden. Viele andere Ameisenarten waren ebenfalls recht weit und gleichmäßig über das Untersuchungsgebiet verbreitet.

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Nur sechs Arten wurden in Einzelexemplaren gefunden. Weder Abundanz der Arten noch Artenzusammensetzung wurden durch die Art des Epiphytenbewuchses beeinflusst. Zweitens wurden auch *in-situ*-Beobachtungen an einer zusätzlichen Gruppe von 34 Bäumen derselben Baumart durchgeführt. Diese Bäume waren entweder mit Epiphyten bewachsen oder epiphytenfrei. Arbeiterinnen wurden mit Thunfisch- und Zuckerködern angelockt, und zwischenartliche Interaktionen sowie die Neststandorte registriert. In dieser Teiluntersuchung wurden 40 Arten bestimmt, die ausnahmslos auch in den Fallen gefunden worden waren. Etwa die Hälfte der Kolonien (48%) befand sich in Totholz und 29% in Epiphyten. Auch hier zeigte sich kein Einfluss des Epiphytenbewuchses auf die Zahl der Arten oder ihre Zusammensetzung, die Korrelation zwischen Ameisenabundanz und Epiphytenbewuchs war aber signifikant. In beiden Teilstudien gab es keine signifikanten Arten-Assoziationen, die Ameisengemeinschaften waren also nicht mosaikartig strukturiert. Aus den Daten kann die Schlussfolgerung abgeleitet werden, dass Epiphyten die Zusammensetzung der Ameisengemeinschaften in den untersuchten Baumkronen kaum beeinflussen, weil Ameisen wahrscheinlich sehr opportunistisch auf unterschiedliche pflanzliche Ressourcen reagieren.

Key words: *Annona glabra* – ant mosaic theory – canopy – insect traps – Panama

Introduction

Due to their extraordinary abundance, ants are a most remarkable component of the tropical arboreal arthropod fauna (Erwin 1983; Hölldobler & Wilson 1990), and are a useful indicator taxon, for example in order to assess overall biodiversity (Longino & Colwell 1997), altitudinal gradients (Brühl et al. 1999), forest edge and fragmentation effects (Majer & Delabie 1999; Dejean & Gibernau 2000), or faunal differences between understory and canopy (Longino & Nadkarni 1990; Yanoviak & Kaspari 2000). Ants may be of major importance for the structure of arboreal arthropod communities, because they exert a constant, high predation pressure (Tobin 1995; Floren & Linsenmair 1997): they have been labeled the 'most important invertebrate predators' in the tropics (Hölldobler & Wilson 1990; Linsenmair 1990).

For more than a century, ant-plant interactions have been a favorite topic in tropical ecology (e.g., Schimper 1888; Janzen 1974; Fiala et al. 1994; Dejean et al. 1995). Epiphytes are frequent partners of such mutualisms (Davidson & Epstein 1989; Benzing 1990), providing living space for ant colonies (domatia) or nutrition from extrafloral nectaries, or both. In return, the plants benefit from nutrients retrieved from the ants' waste, or enjoy protection from herbivores (reviewed in Hölldobler & Wilson 1990). In this paper, however, we investigate whether *non-myrmecophilic* epiphytes also influence ant diversity and abundance in the studied tropical forest canopy. Apart from increasing the structural heterogeneity of the canopy habitat and providing shelter from climatic extremes, some epiphytes could promote ant occurrence by impounding large amounts of leaf litter (Davidson & Epstein 1989; Richardson 1999), which

is an important prerequisite for many canopy-nesting ants (Longino & Nadkarni 1990). Many ant species also nest inside non-myrmecophilic epiphytes (Schimper 1888; Blüthgen et al. 2000). Richards (1996) even claims that epiphytes provide the chief nesting sites for arboreal ants in tropical rainforests. Epiphytes sometimes foster a rich arthropod fauna (Cotgreave et al. 1993; Richardson 1999; Stuntz et al. 2002b), a potential resource for predatory ants. Moreover, epiphytes have a mitigating influence on the microclimatic conditions in their immediate surroundings (Stuntz et al. 2002a). Thus, we hypothesized that epiphytes positively influence ant abundance and diversity. Alternatively, ants may also be indifferent to epiphytes: being highly opportunistic in many respects (e.g., Stork 1987; Blüthgen et al. 2000). The following report, which is part of a series of papers on the influence of vascular epiphytes on canopy arthropods (Stuntz et al. 2002 a, b, 2003), addresses these divergent notions by comparing the ant faunas of tree crowns bearing different sets of epiphyte assemblages, and trees free of epiphytes.

Our study also contributes to the ongoing discussion on the occurrence and importance of ant mosaics in the tropics. Recently, the existence of well-organized ant mosaics was refuted for high-diversity rainforests (Floren & Linsenmair 2000). Most of our knowledge of ant mosaics comes from orchards, mangroves or other areas with little diverse faunas (Room 1971; Leston 1973a; Leston 1973b; Majer 1976; Fox & Fox 1982; Majer 1982; Cole 1983; Adams 1994; Fowler et al. 1998). Thus, we also asked the question whether in our model system of small trees at the forest edge, the ant fauna is mosaic-like structured or rather heterogeneous and unpredictable like the one investigated by Floren & Linsenmair (2000).

Materials and methods

The study was conducted in the tropical moist forest of the Barro Colorado Nature Monument (BCNM, 9°10′N, 79°51′W) in Panama. The area receives approximately 2600 mm of annual precipitation with a pronounced dry season from late December to April. Detailed descriptions of climate and vegetation can be found in Leigh & Windsor (1982).

Study trees and epiphytes

The chosen host tree, *Annona glabra* L., grows abundantly along the shore of Lake Gatún. Despite its rather small stature (mean height of the study trees 4.9 m ± 0.9 SD, n = 25), the climatic conditions in these tree crowns are similar to the upper forest canopy due to its exposure to sun and wind along the shore (Zotz et al. 1999). It is often dominated by a single epiphyte species (Zotz et al. 1999), which allowed us to define distinct tree categories with rather uniform epiphyte assemblages: 1) trees free of epiphytes as control group, 2) trees with the orchid *Dimerandra emarginata,* 3) trees with the large tank bromeliad *Vriesea sanguinolenta,* and 4) trees dominated by the medium-sized bromeliad *Tillandsia fasciculata.* Hereafter, the study species are addressed by their generic names. In order to account for spatial heterogeneity across different locations, we chose sites where trees of all categories grew in close vicinity. *Tillandsia*-trees were found only at four of the seven study sites (distributed all over BCNM), and were sampled only when arthropod abundance was expected to be high. Traps were thus closed during the second half of the rainy season, i.e. from July to November 1998. Consequently, two different data sets were used for comparisons among categories. When the entire sampling period of thirteen months was included, we compared only the categories 1–3, when all four categories were taken into account, we analyzed data from eight months with active traps in all trees.

Trapping and processing the ants

Arthropods were collected with three different types of traps: flight interception traps, branch traps and yellow color traps, which remained in the tree crowns for an entire year and were emptied every two weeks. They are illustrated and described in Stuntz et al. (1999). Branch traps were most effective for capturing ants, yielding more than twice as many specimens than flight interceptors and yellow color traps (Stuntz et al. 1999).

The captured arthropods were transferred to 70% ethanol until further treatment. Ants were separated from the rest of the catch, mounted and identified to genus level with the key of Bolton (1994), then assigned to morphospecies. The reference collection was sent to specialists (Philip S. Ward for the *Pseudomyrmecinae* and John T. Longino for all other subfamilies) for species identification. Vouchers are deposited at the Smithsonian Tropical Research Institute in Panama, and at the Technische Universität München (Freising, Germany).

In situ observation of the ant fauna

We also conducted a bait study in 34 additional *Annona* trees in the same study area. Fourteen trees were free of epiphytes, two were dominated by *Vriesea*, six by *Tillandsia*, and twelve supported a mixed assemblage of epiphyte species (including, e.g., *Tillandsia subulifera* Mez., and *Polypodium crassifolium* L.)

Total ant abundance per tree (irrespective of species identity) was visually estimated during a 10-minute-interval prior to the placement of baits. Five abundance classes were used: class 1 (1–2 ants observed), class 2 (appr. 10 ants observed), class 3 (appr. 100 ants), class 4 (over 100 ants) and class 5 (many hundreds of ants, busy trails on every branch). Then, the ant community composition was studied on each tree at daytime (09:00–17:00 h) by placing tuna and sugar baits on all major branches and stems. During the next two hours, species arriving at the baits as well as all active ants within the tree crown were noted. Ant behavior, such as aggressive interactions with other species, bait monopolization, or worker recruitment was recorded. By visually following ants departing from baits, the location and number of nesting sites was determined. One to ten specimens per species were collected and processed as described above. Similarly, nocturnal activity was also studied on a subset of 18 of the study trees (between 21:00–24:00 h). Species that had monopolized more than 50% of the baits in a particular tree at the end of the observation time were considered dominant on this tree.

Epiphyte biomass and other host tree traits

We estimated epiphyte biomass by measuring either the maximum leaf length of each bromeliad or the length of the youngest stem of each orchid stand, respectively. Biomass and leaf area correlates with those parameters (compare Stuntz et al. 2003). In general, trees with *Dimerandra* had both lower epiphyte biomass and epiphyte leaf area than trees with *Vriesea* or *Tillandsia.* Total epiphyte biomass ranged from 90 g dry mass in a tree with *Dimerandra* to 3,853 g dry mass in a tree with abundant *Tillandsia*, and epiphyte leaf area ranged from 0.21 m² in the same *Dimerandra* tree to 27.9 m² in a tree with *Vriesea*. The median leaf area of a tree was 30 m² (host tree foliage only), compared to 8 m² for epiphytes per tree.

For the *in situ* observations, host tree traits (tree height, crown volume, circumference, stem number) were estimated. As the majority of ants nested in dead wood cavities, the amount of dead wood in a tree crown (mainly dead branches still attached to the tree) was visually estimated and scored at a scale from one to ten (0 = no dead wood; 10 = large amounts of dead wood).

Statistics

Statistical analysis was done with STATISTICA (Stat-Soft Inc., Oklahoma, USA). The numbers of species and individuals of the four tree categories were not normally distributed and thus compared with Kruskal-Wallis-ANOVA (KW-ANOVA). Changes over time were analyzed with repeated-measures ANOVA (RM-ANOVA). A Spearman rank coefficient was used to test for correlations between epiphyte load and ant abundance. Species richness, i.e. the absolute number of species found in one sampling unit, was used as a measure of α-diversity, and the Sørensen index as a measure of β-diversity (Magurran 1988). The Sørensen values in Table 3 were normally distributed and thus allowed the use of parametric one-way ANOVA among categories. To test for differences in the species compositions of the faunas among epiphyte species, we ran multidimensional scaling analyses (MDS) based on a dissimilarity matrix of 1-Sørensen values (Southwood 1978). This multivariate ordination method was favored over factor analysis because no normal distribution of the data is required. Finally, association analyses were computed following the protocol of Ludwig & Reynolds (1988), which uses a series of pairwise comparisons and is based on χ^2-statistics.

Results

I. Trap survey

Composition of the fauna
In total, we collected 22,335 specimens from 91 species in 32 genera and six subfamilies (Table 1). Many species were widespread throughout the study area (Fig. 1): 26 species (29%) were found in more than half of all study trees, eight species occurred in over 90% of the trees, and three of those, *Solenopsis zeteki*, *Pheidole* cf. *flavens* and *Camponotus (Myrmobrachys)* sp. 4 (cf. *auricomas*) occurred on every single study tree. *Solenopsis zeteki* was by far the most abundant species (4,632 specimens) and contributed one fifth of all individuals. Myrmicinae were the most diverse and numerous subfamily (40 species and 15,222 individuals) (Table 1). The most species-rich genera

were *Camponotus* (Formicinae), *Pheidole* (Myrmicinae) and *Pseudomyrmex* (Pseudomyrmecinae) each with ten species.

Comparison of tree/epiphyte categories
α-diversity. During a trapping period of eight months, we collected a median number of 26 (range: 15–38) species and 510 (88–1,039) individuals per tree (n = 25). There were no significant differences in the number of ant species and individuals among categories (Table 2; KW-ANOVA, numbers of species: p = 0.62; numbers of individuals: p = 0.39). To account for seasonal fluctuations, we tested for differences between tree groups over time: data were recorded separately in two-week-intervals and compared with RM-ANOVA. Seasonal variation significantly influenced both the numbers of individuals and species (p < 0.001). Confirming the results of the KW-ANOVA, the tree/epiphyte category did not significantly influence either the number of individuals (p = 0.30) nor species (p = 0.29). There was no interaction between time and tree category (p > 0.55).

At the subfamily level, differences in abundance across tree categories were found in a single taxon: Dolichoderinae were most numerous in *Tillandsia* trees (KW-ANOVA; n = 25; p = 0.049). There, we collected a median number of 139 Dolichoderinae (range: 42–278, n = 4), compared to 37 (13–166, n = 7) in control trees, 34 (15–91, n = 7) in *Dimerandra* trees and only 10 (0–115; n = 7) in *Vriesea* trees. In three of the four trees with *Tillandsia*, hundreds of ants of the genus *Azteca* inhabited (and fiercely defended) most bromeliads, each probably being an outpost of a polydomous colony (Stuntz & Linder, personal observation). The abundance of the other subfamilies was in-
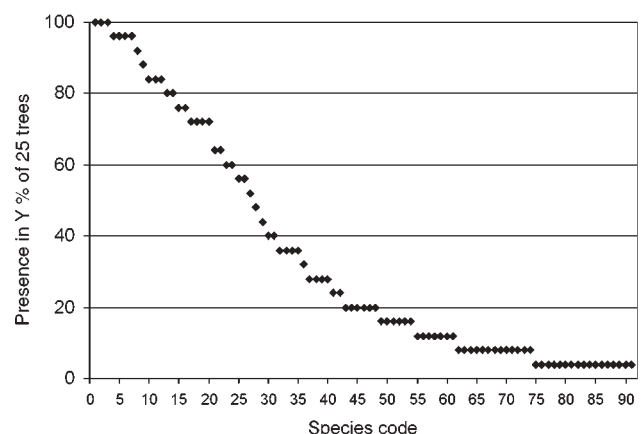

Fig. 1. Rank-abundance plot of ant species. Abundance is defined as the proportion of study trees (n = 25), in which a certain species was collected during a trapping period of one year. For lack of space, the species ranked along the x-axis have been given numbers (see Table 1).

Table 1. Species list. Given are totals of specimens (n) trapped in 25 study trees during the study period. Species marked with an asterisk were also collected during direct observations. The totals of individuals within one subfamily are given in italics, the number of species within a subfamily in parentheses behind the family names. The species codes ('code') are referred to in Fig. 1. Morpho-species names (genus + sp.1, sp.2 etc) relate to our voucher collection or to the collection of J. T. Longino (JTL-001).

Species or morpho-species name	n	code	Species or morpho-species name	n	code
Myrmicinae (40)	*15,222*		**Formicinae (15)**	*1,952*	
Solenopsis zeteki*	4,678	1	Paratrechina sp. 2*	602	27
Wasmannia rochai*	2,293	15	Camponotus (Myrmobrachys) sp. 4 (cf. auricomus)	344	3
Pheidole cf. flavens*	1,893	2	Camponotus atriceps*	301	6
Solenopsis sp. 1*	1,631	10	Paratrechina sp. 1*	220	7
Monomorium floricola*	928	21	Paratrechina sp. 3	181	19
Solenopsis sp. 4	918	13	Camponotus sexguttatus*	154	12
Pheidole punctatisssima*	857	17	Camponotus novogranadensis	52	25
Cyphomyrmex rimosus complex*	567	5	Paratrechina sp. 4	32	32
Crematogaster carinata and brasiliensis* 1)	472	14	Camponotus (Myrmeurynota) sp. 7 (cf. linnaei)*	20	37
Pheidole radoszkowskii pugnax	417	28			
Pheidole cocciphaga*	344	16	Camponotus mucronatus*	14	35
Pheidole sp. 7	29	75	Camponotus senex	10	51
Pheidole radoszkowski luteola	29	44	Brachymyrmex sp. 1*	8	53
Leptothorax echinatinodis	19	38	Camponotus planatus	8	52
Xenomyrmex JTL-001*	17	62	Camponotus (Tanaemyrmex) sp. 1*	5	57
Pheidole sp. 6	17	34	Camponotus sericeiventris	1	82
Pheidole sp. 0	14	55			
Crematogaster brevispinosus crucis	11	45	**Dolichoderinae (9)**	*3,619*	
Pyramica cf. epinotalis	10	76	Azteca cf. velox	1,410	4
Pheidole pubiventris	10	63	Azteca cf. trigona*	1,336	8
Pheidole decem	8	77	Dolichoderus bispinosus*	429	23
Cephalotes grandinosus	7	54	Dolichoderus diversus	407	18
Xenomyrmex panamanus*	6	66	Dolichoderus debilis*	15	41
Atta cephalotes	6	64	Azteca forelii*	10	46
Strumigenys borgmeieri	6	48	Tapinoma melanocephalum*	7	40
Cephalotes umbraculatus	4	68	Dolichoderus lutosus	3	70
Cephalotes atratus	4	67	Dolichoderus laminatus	2	72
Cephalotes minutus	4	58			
Acromyrmex octospinosus*	3	69	**Pseudomyrmecinae**	*543*	
Strumigenys emmae	3	61	Pseudomyrmex elongatus*	241	9
Crematogaster crinosa*	3	60	Pseudomyrmex gracilis*	121	24
Cardiocondyla wroughtonii	3	59	Pseudomyrmex simplex*	85	20
Strumigenys elongata	2	80	Pseudomyrmex ita*	39	31
Rogeria foreli	2	74	Pseudomyrmex filiformis	34	43
Cephalotes setulifer	2	71	Pseudomyrmex oculatus	12	56
Wasmannia auropunctata	1	92	Pseudomyrmex tenuissimus	7	54
Solenopsis sp. 6	1	91	Pseudomyrmex euryblemma	2	79
Solenopsis sp. 5	1	90	Pseudomyrmex boopis	1	88
Megalomyrmex silvestrii	1	84	Pseudomyrmex browni	1	89
Leptothorax antoniensis	1	83			
			Ecitoninae (10)	*572*	
Ponerinae (7)	*427*		Labidus praedator	358	30
Odontomachus bauri*	225	11	Labidus coecus	149	36
Odontomachus ruginodis*	116	22	Neivamyrmex sp. 1	36	29
Pachycondyla harpax	31	49	Neivamyrmex sp. 2	11	42
Hypoponera opaciceps	30	33	Eciton hamatum	10	50
Pachycondyla villosa	18	39	Neivamyrmex pilosus	3	78
Ectatomma ruidum	6	65	Eciton burchelli	2	73
Anochetus inermis group	1	81	Neivamyrmex sp. 3	1	86
			Neivamyrmex sp. 4	1	85
			Nomamyrmex esenbeckii	1	87

[1]) These two species were lumped and assigned to one morphospecies

dependent of the tree category, both in terms of species numbers and individuals (KW-ANOVA, p > 0.1).

The category assignment was merely based on species identity of the prevalent epiphyte in a tree, irre-spective of the quantity of epiphytes in its crown. Therefore we also tested for correlations between epi-phyte biomass and numbers of species and individuals. In neither case did we find a significant relationship

(Spearman rank correlation, numbers of species: p = 0.81; numbers of individuals: p = 0.18). This was also true when analyzing the subfamilies separately (Spearman rank correlation, r between –0.3: Myrmicinae and +0.3: Dolichoderinae, p > 0.1).

β-diversity. Ant assemblages in the four tree/epiphyte categories did not differ in species composition (Fig. 2). The symbols were not grouped corresponding to the four tree categories, but were rather evenly distributed. The Sørensen indices of the ant communities in the four categories were high and ranged from 0.69 (between *Tillandsia* trees and control trees) to 0.83 between trees with *Vriesea* and control trees.

Species assemblages of individual trees did not differ significantly either (Table 3). The Sørensen indices between pairs of epiphyte-laden trees among each other, of control trees among each other and of epiphyte-laden trees paired with control trees did not differ significantly (ANOVA, p = 0.75). Similar results were obtained when including only those species that were present on a minimum of three study trees (to reduce chance effects by the occurrence of rare species; one-way ANOVA, p = 0.87), or when excluding the most abundant species, reasoning that their 'generalist' appearance might blur subtle differences in the composition of less abundant species (one-way ANOVA, p = 0.10; Table 3).

The omnipresent *Solenopsis zeteki* was first-ranked in all four tree categories (Table 4). Of the 19 species

with a minimum of five specimens (median) per tree (during eight months of trapping), three occurred throughout all categories and another three were abundant in three of the four categories. Nine of these 19 species were ranked among the most abundant species in one category alone.

Association calculations for 903 species pairs revealed no significant association between species, neither positively nor negatively (p > 0.05). This suggests that a structured ant mosaic did not exist in our study system.

2. *In situ* observation of the ant fauna

Faunal composition

We collected specimens of 40 species of ants in 20 genera and five subfamilies (Table 1). During two hours of observation, a median of 5 species (range 1–12, n = 34) was recorded per study tree. Most frequently observed was *Odontomachus ruginodis*, which nested on 47% of all study trees, followed by *Solenopsis zeteki*, recorded on 44% of the trees. Fifteen species (38%) were seen on only one tree. All species found during the observations also appeared in the traps.

Dominance and species associations

Twelve species attained dominant status on at least one tree (i.e., occupied over 50% of all baits in a given tree at the end of the observation period; Table 5). Association calculations were conducted between ant species of the 34 *Annona* trees. To minimize chance effects, only species occurring on a minimum of five trees were included. Three species pairs showed a positive association (*Camponotus atriceps/Crematogaster* cf. *carinata* (association coefficient C = 0.40); *Camponotus atriceps/Paratrechina* sp. 1 (C = 0.68); *Camponotus sexguttatus/Paratrechina* sp. 1 (C = 0.68)).
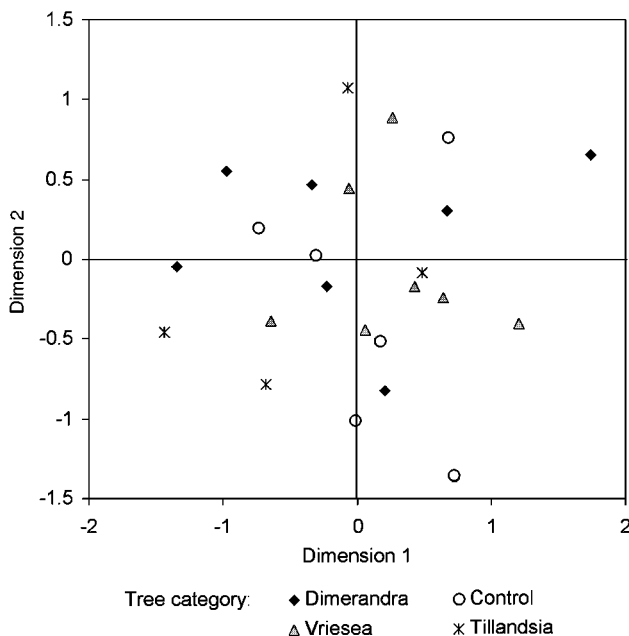
Fig. 2. Multidimensional scaling analysis of the ant assemblages of the four tree/epiphyte cagories. The ordination is based on a dissimilarity matrix (1-Sørensen) of the faunas of 25 study trees; each symbol represents one tree. Ants were collected with 125 traps during eight months.
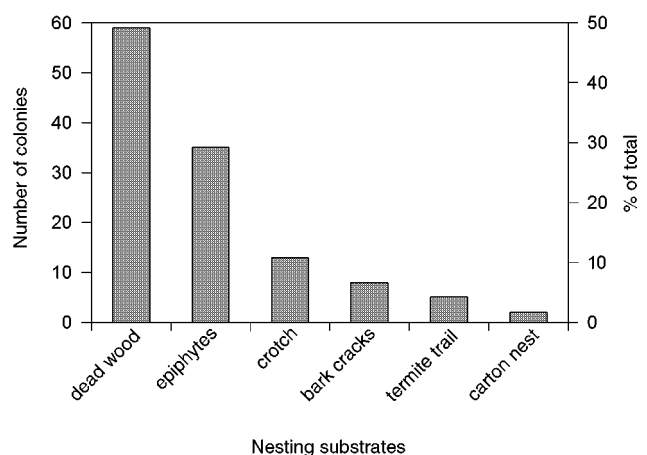
Fig. 3. Nesting substrates used by arboreal ants in *Annona glabra*. In total, we documented the nesting sites of 122 colonies in 34 study trees.

None of these associations was exclusive nor obligate. There were no negative associations between dominant species, and the latter did not maintain mutually exclusive territories.

The influence of epiphytes and other habitat traits

The presence of epiphytes in the study trees had no influence on ant species diversity (KW-ANOVA, p = 0.99).

Epiphyte biomass was positively correlated with estimated ant abundance (Spearman rank correlation, p = 0.045), but not with species richness (Spearman rank correlation, p = 0.49). Species composition was also independent of epiphyte load in the *Annona* trees, as revealed by MDS (not shown). The amount of dead wood in a tree crown showed a significant correlation with ant species richness (Spearman rank correlation,

Table 2. Numbers of ant individuals and species in the 25 study trees. Given are median values, minima and maxima of ants collected in n trees during a period of eight months.

	Control trees	Trees with *Dimerandra*	Trees with *Tillandsia*	Trees with *Vriesea*
Individuals per tree				
Median	272	376	679	510
Min	88	297	436	269
Max	1,039	955	1,014	913
Species per tree				
Median	26	27	22	29
Min	17	15	19	21
Max	38	35	30	35
n	7	7	4	7

Table 3. Average Sørensen values (means ± SD) and statistics of 300 pair wise comparisons among study trees. 'Only abundant species' includes only species that were present on at least three trees, and 'only rarer species' excludes species that were present on more than twenty study trees.

Comparison	Epiphyte-laden trees among each other	Epiphyte-laden trees with control trees	Control trees among each other	ANOVA p-level
All species	0.56 ± 0.08	0.55 ± 0.08	0.54 ± 0.08	0.75
Only abundant species	0.59 ± 0.09	0.58 ± 0.09	0.57 ± 0.09	0.87
Only rarer species	0.44 ± 0.11	0.42 ± 0.11	0.39 ± 0.12	0.10
n pair wise comparisons	153	126	21	

Table 4. Rank order and abundance (n = median) of the most abundant species in the four tree categories. Included are species of which at least five individuals (median) per tree were trapped during eight months. Species present in all four categories are displayed in **bold** script, and species occurring in three of the four categories are underlined.

Control trees	n	Trees with *Dimerandra*	n	Trees with *Tillandsia*	n	Trees with *Vriesea*	n
Solenopsis zeteki	96	*Solenopsis zeteki*	64	*Solenopsis zeteki*	221	*Solenopsis zeteki*	55
Camponotus sp.4)*	18	*Monomorium floricola*	53	*Azteca* cf. *velox*	139	*Pheidole* cf. *flavens*	52
Azteca cf. *velox*	13	*Solenopsis sp.4*	47	*Azteca* cf. *trigona*	37	*Solenopsis sp.1*	22
Dolichoderus diversus	12	*Pheidole punctatisssima*	36	*Pheidole* cf. *flavens*	19	*Azteca* cf. *trigona*	9
Camponotus atriceps	11	*Pheidole radosz. pugnax*	29	*Paratrechina sp.1*	11	*Odontomachus bauri*	8
Pheidole cf. *flavens*	11	*Pheidole* cf. *flavens*	14	*Camponotus sp.4**	7	*Pheidole punctatisssima*	8
Azteca cf. *trigona*	10	*Dolichoderus diversus*	13	*Cyphomyrmex rim. compl.*	6	*Camponotus atriceps*	7
*Crematogaster carinata and brasiliensis***)	10	*Dolichoderus bispinosus*	11	*Solenopsis sp.1*	6	*Cyphomyrmex rim. compl.*	5
Pseudomyrmex elongatus	6	*Pseudomyrmex gracilis*	10	*Pseudomyrmex elongatus*	6		
		*Camponotus sp.4**	9	*Camponotus atriceps*	5		
		Solenopsis sp.1	7				
		Azteca cf. *trigona*	6				

*) *Camponotus (Myrmobrachys) sp.4 (cf. auricomus)*
**) These two species were lumped and assigned to one morphospecies

Table 5. Dominant ant species in *Annona glabra*. Dominance was inferred when a species occupied over 50% of all baits in a given tree at the end of an observation period.

Species	dominant on n trees
Azteca cf. *trigona*	2
Azteca forelii	4
Camponotus (Myrmeurynota) sp. 7 (cf. *linnaei*)	2
Camponotus atriceps	1*
Dolichoderus bispinosus	1
Monomorium floricola	1
Odontomachus ruginodis	3*
Odontomachus bauri	1
Paratrechina sp. 1	1
Paratrechina sp. 2	4
Pheidole punctatisssima	1
Solenopsis zeteki	3

* species active mostly nocturnally

r = 0.4; p = 0.008). Other host tree parameters like tree height or crown volume were not correlated with ant diversity (p > 0.3).

Nesting sites
The studied tree crowns provided a variety of substrates that were used as nesting sites (Fig. 3). The majority of colonies nested in dead wood (48%), another large fraction of ant nests were found inside *Vriesea* and *Tillandsia* epiphytes (29%). One dominant species, *Azteca* cf. *trigona* built large carton nests. A few small species, e.g. *Solenopsis zeteki*, nested in cracks of the fissured *Annona* bark, others used abandoned, carton-covered termite trails. Many *Odontomachus*-colonies nested in crotches close to the water surface. Ants of the genus *Pseudomyrmex* usually built their nests in thin tips of dead branches in the crown periphery. The epiphyte-nesting ant species were rather unspecific in respect to their hosts: nine of the twelve species nesting in epiphytes were also present in control trees without epiphytes, mostly nesting in dead wood.

Discussion

Annona glabra as model system for tropical canopies?
Annona glabra seems to be a feasible model system for the forest canopy, at least for ants. Both overall diversity (91 species) and average species richness per tree (26 species) were within the range of the species numbers reported in previous studies of tropical canopies (e.g. Floren & Linsenmair 1994: 30–40 species per tree in Malaysia; Majer 1994: 91 species in total from a Brazilian cocoa plantation; Majer et al. 2000: 14 species per tree in Brazilean rainforest). In the canopy of *Luehea seemanii* Triana & Planch, a tall tree (Croat 1978), Montgomery (1985) found 22–35 species of ants per tree on Barro Colorado Island. More evidence that the ant fauna in *Annona* is comparable to the one in the forest canopy comes from Yanoviak & Kaspari (2000). They found 32 ant species on baits in the crowns of four emergent tree species in BCNM, 27 of which could be identified to species level: 63% of these species were also common in our samples.

Dominants, submissives and mosaics
Methodological considerations. Many ant communities have clear hierarchies, featuring few dominant species and several subordinate species (e.g., Leston 1973a; Hölldobler & Wilson 1990). The dominance of an ant species cannot necessarily be deduced from its massive occurrence in insect traps, but rather involves a characteristic behavior towards co-occurring species. Dominants as consistently aggressive to workers of all other species, whereas those of the subordinate species avoid dominants (Hölldobler and Wilson 1990). Frequently, ant species are considered dominant if they are capable of monopolizing bait, i.e. of defending food resources successfully against other species (Yanoviak & Kaspari 2000). Trap yields may still reasonably reflect dominance, because dominants have large colonies and quickly recruit many workers to food resources (e.g., Leston 1973a; Hölldobler & Wilson 1990). This higher activity should be reflected in greater abundance in the traps. Correspondingly, 88% of the species in the present study that were observed to monopolize baits (15 of 17 species), were among the most abundant species caught in the traps and were captured in over 50% of all study trees.

Studies with insect traps (as with insecticidal knockdown) also yield an unknown number of 'tourists' or 'transient species' (*sensu* Stork 1987), i.e. taxa not genuinely associated with the trees in which they were trapped. An example for such transient species are the ten species of army ants (Ecitoninae), or the leaf cutters *Atta cephalotes* and *Acromyrmex octospinosus* (Table 1): these are obligate ground nesters obviously only foraging in the study trees. If the 'tourist' fraction is large, subtle patterns in species diversity might easily be blurred. Our *in situ* observations reduced this problem. During only 82 hours of observation, we documented local nesting sites for 40 of the 91 species collected during one year (i.e., over almost 8800 hours) of trapping. Only the rarer species and the 'transients' (e.g. the ten army ant species) were not recorded during direct observations (Table 1). Overall, the results of the observations confirmed the outcome of the trap survey, both in terms of the (non-detectable) influence of epiphytes on the ant fauna and the lack of an ant mosaic.

Ant mosaics. Since Leston (1973a) originally described the phenomenon of an 'ant mosaic', there have been numerous accounts of mosaic-structured ant communities (reviewed in Hölldobler & Wilson 1990). However, most of the information on these highly deterministic and predictable communities comes from locations with a somehow impoverished fauna, e.g., African and Brazilian cocoa farms (Room 1971; Leston 1973b; Majer 1976), mangroves (Cole 1983; Adams 1994), or tropical Australia (Fox & Fox 1982; Majer 1982), which is known for its little diverse ant fauna (Majer 1990).

The ant fauna studied here was not mosaic-like structured. Dominant ants neither had a set of favored subordinates typical for a mosaic nor did they consistently exclude other dominants yielding mutually exclusive territories. In contrast, Berghoff, Zotz & Linsenmair (unpubl. observ.) found mosaic-like structured ant assemblages on *Annona glabra* trees bearing the epiphytic orchid *Caularthron bilamellatum* (Rich.f.) Schult. This orchid is a true myrmecophyte, providing nesting space in its hollow pseudobulbs and nutrition from extrafloral nectaries. According to Jackson (1984), ant mosaics are often established around a predictable food source. While none of our study epiphytes supplied extrafloral nectar, *Caularthron* guaranteed a year-round supply of nourishing exudates. As nectar is the main diet of most canopy dominants (Leston 1973a; Kaspari 1993), the orchid's nectaries may provoke vital interspecific competition. In contrast, the absence of such strong deterministic forces might allow a less hierarchic, more stochastic array of ant species. Hölldobler & Wilson (1990) noted the worldwide tendency that true dominants occur only in regions where faunas as a whole are small (boreal Europe, small islands, orchards). If species poorness is a prerequisite for the establishment and maintenance of ant mosaics, their occurrence is unlikely in very species-rich ecosystems like the Malayan rainforest canopy (Floren & Linsenmair 2000) or the one we studied.

Epiphytes and ants

Epiphytes dwelling in the crowns of the study trees had no effect on the latter's arboreal ant fauna. Diversity measures were not influenced by the type or amount of epiphytes in the respective crown, neither was ant abundance (Table 2–4, Fig. 2). There is a wealth of information about positive (although often facultative) interactions between ants and ant-plants in the tropics (e.g., Schimper 1888; Wheeler 1942; Janzen 1974). The present study investigated whether non-myrmecophilic epiphytes also contribute to ant diversity by increasing the structural heterogeneity of the canopy habitat and by providing shelter from climatic extremes and predators. However, only 29% of the observed ant colonies nested inside the non-myrmecophilic epiphytes *Tillandsia* and *Vriesea* (Fig. 3), whilst 48% preferred dead wood as substrate. This observation strongly disagrees with Richards' (1996) notion that epiphytes provide the chief nesting sites for arboreal ants in tropical rainforests. Ants readily use the available infrastructure provided by epiphytes in tropical canopies, but are opportunistic in the use of alternatives: most of the species nesting within epiphytes were also present on trees free of epiphytes, where they mostly used dead wood. A similarly opportunistic use of nesting options in epiphytic bromeliads is reported by Blüthgen et al. (2000) for a Venezuelan lowland forest.

Conclusion

Epiphytes had no significant influence on either α-diversity nor β-diversity of ants. Several of the most abundant ant species showed typical dominant behavior in the study trees, but the lack of interspecific associations suggests that the community as a whole was not arranged in a well-organized ant mosaic. We conclude that non-myrmecophilic epiphytes in tropical tree crowns, although readily used as nesting sites and shelter, do not influence local or between-habitat diversity of ants. Instead, ants seem to be highly opportunistic with respect to their host plants.

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